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Using otolith chronologies to identify extrinsic drivers of growth of 2 commercially targeted small pelagic fish species

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Abstract—Climate variability is a major cause of changes in marine ecosystems, including changes in both the environment and in many fish species. Understanding the factors influencing key biological characteristics, such as growth, is important for commercially targeted species because these characteristics are used in stock assessments that inform fisheries management. In this study, otoliths were used to examine the growth rates and growth chronologies of 2 commercially targeted small pelagic fish species, the common jack mackerel (*Trachurus declivis*) and redbait (*Emmelichthys nitidus*), from 2 regions of southeastern Australia. Both species grew larger off Kangaroo Island (common jack mackerel: asymptotic length [L_∞]=299.40; redbait: L_∞=259.79) than off southern New South Wales (common jack mackerel: L_∞=249.52; redbait: L_∞=238.89). Temporal growth synchrony in both species and regions (0.17–3.50%) was low compared with that of more-site-attached benthic species. Interannual variations in growth rates of common jack mackerel off Kangaroo Island were positively correlated with sea-surface temperature (SST), with growth rates 18% higher at 18.0°C than at 16.4°C. However, growth was not correlated with SST or chlorophyll-*a* concentration for the other species and locations. Developing a more complete understanding of the environmental drivers of growth in these small pelagic fish species may require chronologies to be extended and extrinsic variables in the models to be increased.

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Small pelagic fish species are a diverse group of marine species that form large, mobile epipelagic schools and constitute the majority of the vertebrate biomasses in most open-water ecosystems (Agenbag et al., 2003; Fréon et al., 2005). They form a pivotal link between upper and lower trophic levels, facilitating energy transfer from plankton to predators, such as marine mammals, seabirds, and large fish species (Essington et al., 2015). Disruption or alteration of this link can have broad effects on marine ecosystems (Essington et al., 2015). Small pelagic fishes also support some of the largest fisheries in the world. For example, the fishery that targets Peruvian anchoveta (*Engraulis ringens*) in the Humboldt Current is responsible for Peru having one of the largest total marine catches in the world (FAO, 2018).

Somatic growth of small pelagic fishes is highly variable and related to their reproduction, abundance, movement patterns, and mortality (Rountrey et al., 2014; Lorenzen, 2016). For example, the growth of the Atlantic horse mackerel (*Trachurus trachurus*) varies across its distribution, with growth rates and length at maturity increasing with latitude (Abaunza et al., 2008). Understanding drivers of growth variation is crucial for determining how the population dynamics of small pelagic fishes may vary over space and time (Doubleday et al., 2015; Smoliński, 2019). Predicting how populations will adapt to environmental changes and adjusting fishing strategies accordingly will help prevent overfishing (Black, 2009). For example, dominant regime shifts between sardine (*Sardinops* spp.) and anchovy (*Engraulis* spp.) species have been attributed to differences in the optimum temperature for growth (Lindegren et al., 2013), influencing future fish stocks and fisheries development (Koenigstein et al., 2016).

Age and growth are key characteristics in fisheries research and critical components of age-structured population models (Fournier et al., 1998). Growth chronologies of fish species

can be constructed by examining otoliths, metabolically inert calcified structures that provide information about biological events and environmental conditions throughout a fish's life (Campana, 1999). The width of an otolith increment can be linked to the somatic growth rate of a fish (Ashworth et al., 2017). Ambient factors (e.g., temperature and food availability) influence the physiology and somatic growth rates of fishes. The width of growth increments (pairs of opaque and translucent bands) fluctuates in response to variations in growth rates (Morales-Nin, 2000; Kerr and Campana, 2014). Age and growth models have been developed to produce growth increment chronologies that can be used to investigate abiotic and biotic factors influencing growth (Black et al., 2005; Morrongiello and Thresher, 2015).

Growth chronologies have been applied to a range of fish species, including the black bream (*Acanthopagrus butcheri*) (Doubleday et al., 2015), the sand whiting (*Sillago ciliata*) (Stocks et al., 2011), species of ocean perch (*Helicolenus* spp.) (Grammer et al., 2017), the Atlantic horse mackerel (Tanner et al., 2019), the Atlantic herring (*Clupea harengus*) (Smoliński, 2019), and the snapper (*Chrysophrys auratus*) (Martino et al., 2019), to investigate the effects of climatic events, climate change, and environmental conditions on fish growth (Izzo et al., 2016; Mazloumi et al., 2017; Barrow et al., 2018). However, most studies in which this method was used have focused on benthic and estuarine species that tend to be more site-attached, with few growth chronology studies done on highly mobile, pelagic fishes (Smoliński, 2019).

In Australia, mid-water trawl and purse-seine nets are used in the Commonwealth small pelagic fishery 6–370 km (3–200 nmi) offshore between southwestern Western Australia and southern Queensland (Ward and Grammer[1]). The fishery targets spotted chub mackerel (*Scomber australasicus*); common jack mackerel (*Trachurus declivis*), also known as greenback horse mackerel; redbait (*Emmelichthys nitidus*); and Pacific sardine (*Sardinops sagax*) (Ward and Grammer[1]). The catch of the small pelagic fishery in 2018–2019 has been estimated at around 10,000 metric tons, which is approximately 5% of the annual fishery production in Australia (Steven et al.[2]). The harvest strategy for the fishery includes the use of fishery-independent surveys that follow the daily egg production method for each species, along with catch and effort data, to determine total allowable catch limits (AFMA[3]).

The common jack mackerel is a schooling pelagic species distributed across the temperate coastal waters of southern and southeastern Australia, ranging from Queensland to Western Australia (Gomon et al., 2008). The species is most commonly found over the continental shelf and outer shelf margin in depths of 20–300 m, but it can be found to depths of 500 m (Pullen and TDPIF, 1994). In Australia, the existence of 2 populations of common jack mackerel has been suggested (Ward and Grammer[1]); however, the movement patterns of common jack mackerel have been examined in no studies. The redbait is a schooling pelagic species occurring worldwide in tropical and temperate waters over continental shelfs and in association with seamounts, mid-ocean ridges, and islands (Welsford and Lyle, 2003). This species is commonly found in depths of 100–400 m but can be found to depths of 800 m (Welsford and Lyle, 2003). In no studies have the movements or stock structure of redbait in Australia been assessed (Ward and Grammer[1]). Long-term trends of abundance of common jack mackerel have changed over time with a shift in the dominant small pelagic species from common jack mackerel to redbait in the 1990s (McLeod et al., 2012). It has been suggested that this shift in abundance may be driven by environmental change in the region (McLeod et al., 2012), raising questions over how these changes may affect other aspects of their population dynamics, such as their growth.

Different oceanographic features are likely to influence the growth of small pelagic fish across their range off Australia. Along the southeastern coast of Australia, the Pacific Ocean is influenced by the El Niño–Southern Oscillation and Interdecadal Pacific Oscillation, phenomena that result in changes in rainfall, SST, and trade wind strength (Fiedler, 2002; Overland et al., 2010). In addition, the East Australian Current (EAC) is a key oceanographic feature that moves warm, nutrient-poor water south along eastern Australia (Ridgway, 2007; Ridgway and Hill[4]; Suthers et al., 2011). Originating in the Coral Sea with a southward flow, the EAC eventually forms the Tasman Front and a southward flowing eddy field (Ridgway and Hill[4]; Suthers et al., 2011). In contrast, southern Australia, bordered by the Indian Ocean, has strong coastal upwelling along the Bonney Coast, western Kangaroo Island (KI), and the southern coast of Eyre Peninsula, transporting cold, nutrient-rich waters to the surface (Kämpf et al., 2004; Middleton and Bye, 2007; Neuheimer et al., 2011).

To examine if local environmental influences may be affecting the growth patterns of small pelagic fishes, growth chronologies were produced from otolith increments of 2 commercially targeted small pelagic fish species—the common jack mackerel and redbait—from 2 regions off southeastern Australia. Using a combination of length-at-age modeling and growth chronology mixed-effects modeling, we compared the growth rates of these

[1] Ward, T. M., and G. L. Grammer. 2018. Commonwealth small pelagic fishery: fishery assessment report 2017. Report to the Australian Fisheries Management Authority. South Aust. Res. Dev. Inst., SARDI Publ. F2010/000270-9, SARDI Res. Rep. Ser. 982, 114 p. SARDI Aquat. Sci., Adelaide, Australia. [Available from website.]

[2] Steven, A. H., D. Mobsby, and R. Curtotti. 2020. Australian fisheries and aquaculture statistics 2018, 135 p. Fish. Res. Dev. Corp. Project 2019-093. Aust. Bur. Agric. Resour. Econ. Sci., Canberra, Australia. [Available from website.]

[3] AFMA (Australian Fisheries Management Authority). 2019. Annual report 2018–19, 169 p. Aust. Fish. Manage. Auth., Canberra, Australia. [Available from website.]

[4] Ridgway, K., and K. Hill. 2009. The East Australian Current. *In* A marine climate change impacts and adaptation report card for Australia 2009 (E. S. Poloczanska, A. J. Hobday, and A. J. Richardson, eds.), Natl. Clim. Chang. Adapt. Res. Facil. Publ. 05/09, 16 p.

species and investigated potential environmental drivers of their growth. Specifically, in this study, we 1) compared growth rates of each species between KI, South Australia, and New South Wales (NSW) and 2) investigated the influence of local environmental conditions on the growth rates of both species in each region.

Materials and methods

Study sites and sample collection

Common jack mackerel and redbait were collected from 47 trawl tows at depths between 100 and 303 m off KI and from 49 trawl tows at depths between 60 and 283 m off southeast NSW throughout each year between 2014 and 2016; the samples were taken from catch of a single mid-water trawling vessel that is part of the Commonwealth small pelagic fishery (Fig. 1). From the haul of each trawl tow, 50 fish of each species were randomly selected and frozen. Fish were then subsampled (10 fish per trawl sample) for age and growth analysis, in the laboratory; fork length (FL, in millimeters), total weight (in grams), and sex were recorded, and otoliths were extracted.

Otolith preparation and increment analysis

Sagittal otoliths were removed from each fish, rinsed with water, and air-dried. Otoliths were batch embedded in clear epoxy resin and thin-sectioned (sections were ~300 µm) by using a single-blade sectioning saw (Gemmasta[5], Shell-Lap Supplies, Adelaide, Australia) through the primordium (i.e., core) (Fig. 2). Up to 3 transverse sections were taken from each otolith to ensure that a section was taken through the core. Sections were mounted on glass slides, polished, and viewed by using a stereo microscope (3.2× magnification; Olympus SZX7, Olympus Corp., Tokyo, Japan).

To ensure aging accuracy and count reproducibility prior to aging otoliths, the readers were trained with a reference library containing 100 otoliths of known ages for each species. The ages at capture of the fish caught for this study were within the age range for otoliths in the reference library. All otoliths were aged by 2 individuals with extensive experience in aging both species (coefficient of variation of <5%), providing a third reader

[5] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

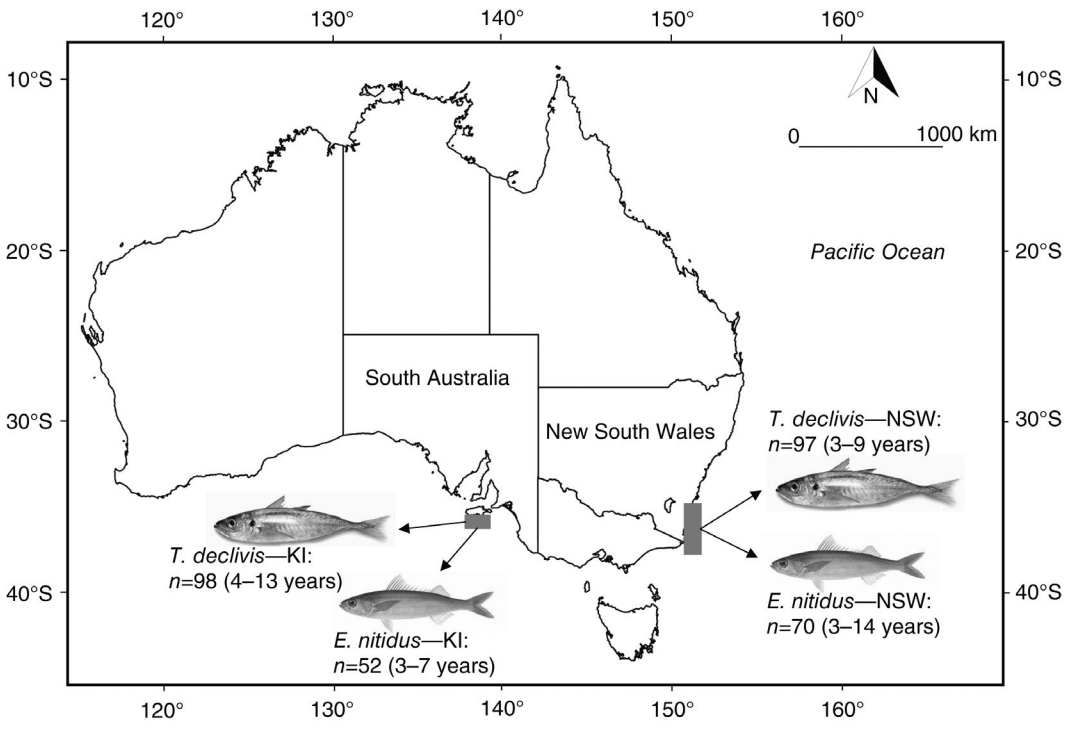

Figure 1

Map of sampling areas (indicated with gray rectangles) where common jack mackerel (*Trachurus declivis*) and redbait (*Emmelichthys nitidus*) were collected by a mid-water trawling vessel off Kangaroo Island (KI) and New South Wales (NSW) in Australia during 2014–2016. Sample sizes (n) and age ranges are provided for the fish sampled for each species in each region.

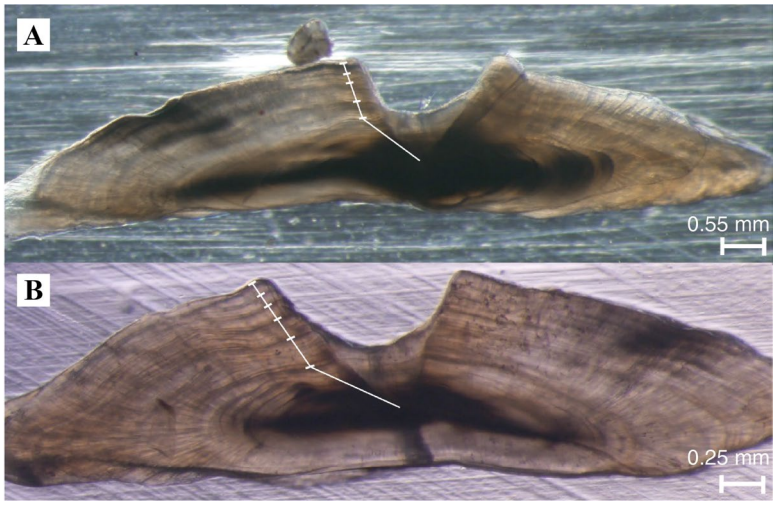

Figure 2

Photographs of thin sections of otoliths from (**A**) redbait (*Emmelichthys nitidus*) and (**B**) common jack mackerel (*Trachurus declivis*) collected off Kangaroo Island and New South Wales in Australia between 2014 and 2016. Images are shown at 3.2× magnifications under transmitted light. The white line indicates the location of measurement, and the horizontal white markings along the line indicate annual growth rings.

with a reference age for increment measurement. Otoliths were viewed under both reflected and transmitted light without focal adjustment or movement of the slide. Photographs were taken (with an Olympus DP73 digital microscope camera, Olympus Corp.) with the light sources overlaid on each other to enhance contrast and visibility of growth increments and allow increments to be accurately identified.

Annual deposition of growth bands has been validated in common jack mackerel by using bomb radiocarbon analysis (Lyle et al.[6]) and in redbait by using marginal increment analysis (Ewing and Lyle, 2009). These validations confirm that each growth increment, composed of a translucent zone and an opaque zone, represents 1 year of growth. Starting from the core, increment boundaries were delineated at the outermost edge of each opaque zone (Fig. 2), by using the image analysis software Olympus Stream (vers. 1.9.1, Olympus Corp.). The distance from the core to the first increment (which equates to growth from hatching to the first birthday; age 0) and from the final increment to the proximal edge (marginal increment) were excluded from all analysis because they did not represent a full year of growth. On the basis of the timing of spawning, a birthdate of 1 January was assigned for common jack mackerel and a birthdate of 1 October was assigned for redbait (Ewing and Lyle, 2009; Ward et al., 2016). Each increment was then assigned a calendar year of formation, back calculated from the capture date.

Growth analysis

The AquaticLifeHistory package (vers. 0.0.9000; Smart et al., 2016; Smart, 2019) was used in the statistical program R (vers. 3.4.0; R Core Team, 2017) to estimate growth parameters for all otoliths from each species and sampling location by fitting length-at-age data with the von Bertalanffy growth function (von Bertalanffy, 1938; Beverton and Holt, 1957):

$$L_t = L_0 + (L_\infty - L_0)(1 - e^{(-kt)}),$$

where t = age in years;
L_t = length at age t;
L_0 = the length at age 0 (fixed at 0);
L_∞ = asymptotic length; and
k = the growth completion parameter.

The von Bertalanffy growth function was fit by using the nls function in R. Differences in growth between sampling locations were then compared for each species by using a likelihood-ratio chi-square test (Ogle, 2016).

Chronologies and environmental variables

The growth chronology data set was truncated for years for which less than 5 increment measurements were available (Morrongiello and Thresher, 2015). A set of generalized linear mixed-effects models were fitted with a gamma error structure and a log-link function. These were used to investigate the sources of growth variation, both intrinsic and extrinsic, within species and regions (Table 1) (Morrongiello and Thresher, 2015). Sea-surface temperature and chlorophyll-*a* (Chl-*a*) concentration (used as proxy for productivity) were both included as extrinsic variables because they have been proven to influence the physiology and somatic growth of fishes (Hughes et al., 2017). Local SSTs and Chl-*a* concentrations were obtained by defining boundary coordinates around all trawl tow positions for each region in the Integrated Marine Observing System of the Australian Ocean Data Network (IMOS[7,8]). Sea-surface temperatures were obtained as 1-day composite data from polar-orbiting satellites (IMOS[7]) and then averaged to produce annual means. Chlorophyll-*a* concentrations were obtained from daily satellite images computed

[6] Lyle, J. M., K. Krisic-Golub, and A. K. Morison. 2000. Age and growth of jack mackerel and the age structure of the jack mackerel purse seine catch. Fish. Res. Dev. Corp. Final Rep., Proj. 1995/034, 49 p. Tasman. Aquac. Fish. Inst., Mar. Res. Lab., Univ. Tasman., Taroona, Australia. [Available from website.]

[7] IMOS (Integrated Marine Observing System). 2018. IMOS-SRS-SST-L3S-single sensor-1 day-day and night time-Australia. [Available from website, accessed December 2018.]

[8] IMOS (Integrated Marine Observing System). 2018. IMOS-SRS-MODIS-01 day-Chlorophyll-a concentration (OC3 model). [Available from website, accessed December 2018.]

Table 1

A list of the variables used in mixed-effects modeling to investigate the sources of growth variation in common jack mackerel (*Trachurus declivis*) and redbait (*Emmelichthys nitidus*) collected off Kangaroo Island and New South Wales in Australia between 2014 and 2016. Environmental data were collected for the period 2002–2016.

Variable	Description	Source
Age	Fish age (in years) when growth increment was formed	
AgeCap	Fish age (in years) when caught	
Year	Year of growth increment formation	
YearClass	Birth year of fish	
FishID	Fish identification number	
SST	Mean annual sea-surface temperature (°C)	IMOS[7]
Chl-*a*	Mean annual chlorophyll-*a* concentration inferred from relative fluorescence per unit volume of the water body (in milligrams per cubic meter)	IMOS[8]

through the OC3M algorithm (IMOS[8]), and Chl-*a* levels were also averaged to produce annual means.

All fixed effects were mean centered to assist in interpretation of interaction terms and model convergence (Morrongiello and Thresher, 2015). All fish determined to have ages ≤2 years were excluded from analysis because, with the first increment being excluded for all fish, only a single increment measurement would be available for these individuals, and a single increment is insufficient to predict growth. The Akaike information criterion corrected for bias from small sample sizes (AIC_c) was used to rank models, and AIC_c weight was used to assess model likelihood: the smaller the weight, the lower the probability the model was "true" on the basis of the included candidate models (Burnham and Anderson, 2004). Marginal and conditional coefficients of multiple determination (R^2) were used as a measure of goodness of fit, and the contribution of the fixed effects (marginal R^2) and the fixed and random effects (conditional R^2) were used to explain variance of the response variable when added to the model (Nakagawa and Schielzeth, 2013).

The optimal model explaining variation in fish growth (i.e., increment width) was determined by using a 2-step process whereby the best random-effect variables (*Year* and *YearClass*) were selected by sequentially adding them in increasing complexity to the models containing the full fixed-effect structure (i.e., the effects *Age* and *AgeCap* were included) through the use of the restricted maximum likelihood estimates of error (Zuur et al., 2009). The combination of models included *Year* and *YearClass* as random intercepts and used these same variables with *Age* included as a random slope on these variables. Random slopes of *Age* were included to allow greater flexibility in growth estimations from the model and to remove age-dependent trends during the analysis. Inclusion of *Year* as a random intercept was intended to be equivalent to the use of traditional dendrochronology, enabling annual estimates of whether growth was high or low as a result of the environmental covariates in relation to the long-term mean (Morrongiello and Thresher, 2015). Similar to the use of *Year*, *YearClass* was used as a random intercept to estimate growth conditions for a group of fish (year cohorts) over their lifetime. *FishID* with a random *Age* slope was included in all models as a random intercept to allow the growth of each fish to vary beyond the model average by inducing a correlation among increment measurements within an individual.

Estimates of the temporal similarity in growth (growth synchrony) were calculated with the interclass correlation coefficient. By using the full intrinsic effects model fit with *Year* intercept and *YearClass* intercept only, the correlation of growth increments among individuals was calculated. Growth chronologies were produced by extracting best linear unbiased predictors for each combination of species and region based on *Year* (variation in growth relative to the long-term mean) and *YearClass* (variation in growth conditions for a group of fish, i.e., year cohorts, over their lifetime relative to the long-term mean) (Morrongiello and Thresher, 2015).

The best fixed effects (*Age*, *AgeCap*, or *Age* and *AgeCap*) were then identified by sequentially adding them in increasing complexity to the selected best random-effect variables. Random-effect variables were initially selected by using maximum likelihood estimates of error, and then they were refit with restricted maximum likelihood estimates of error to produce unbiased parameter estimates (Zuur et al., 2009). Once the optimal intrinsic model was identified, environmental variables were fit as fixed effects to relate the variability in growth to the extrinsic covariates.

All analyses were performed in R, with the packages lme4 (Bates et al., 2015), effects (Fox, 2003), and AICcmodagv (Mazerolle, 2015).

Results

A total of 247 common jack mackerel and 248 redbait from trawl tows conducted south of KI were aged, and 760 common jack mackerel and 342 redbait from southeast NSW were aged. Age across both regions ranged from 1 year to 15 years for common jack mackerel and from 0+ to 14 years for redbait. From these aged samples, a subset of randomly selected otoliths was measured for growth chronology analyses (Fig. 1). A combined total of 1674 increments on otoliths from 195 common jack mackerel (KI: 662 increments, birth years 2003–2012; NSW: 425 increments, birth years 2007–2014) and on otoliths from 122 redbait (KI: 177 increments, birth years 2008–2012; NSW: 410 increments, birth years 2001–2012) were measured, with the greatest number of individuals born between 2007 and 2012 (Fig. 3). Years that corresponded to fish that had otoliths with <5 increments were removed from the

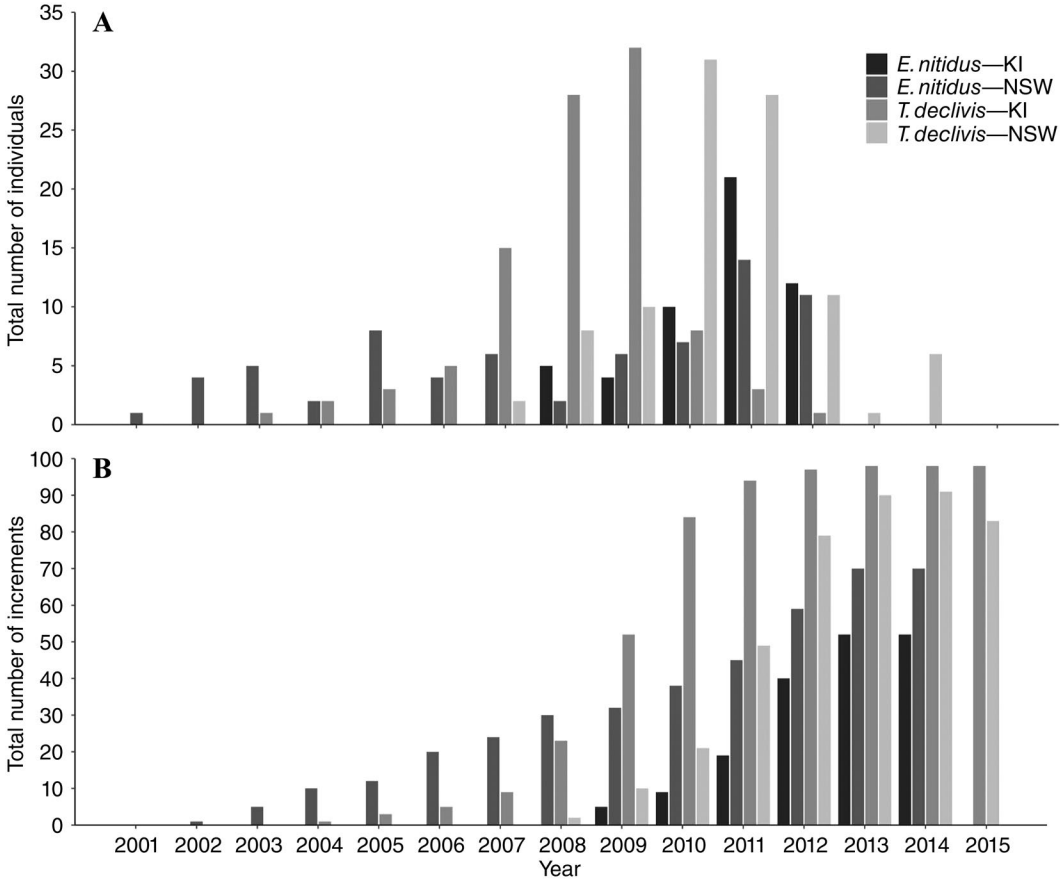

Figure 3

(**A**) Number of common jack mackerel (*Trachurus declivis*) and redbait (*Emmelichthys nitidus*) measured for each birth year and (**B**) number of otolith increments for each calendar year by species and region. These numbers indicate growth chronologies for samples collected during 2014–2016 from waters off Kangaroo Island (KI) and New South Wales (NSW) in Australia.

analyses, resulting in growth chronologies for the periods from 2005 through 2016 for common jack mackerel and from 2003 through 2015 for redbait.

Growth analysis

Estimates of von Bertalanffy growth parameters were significantly different between regions for both species (common jack mackerel: χ^2=310.46, P<0.001; redbait: χ^2=65.90, P<0.001; Fig. 4), with fish from KI (Table 2) growing slower but having a higher asymptotic length than fish caught in NSW (Table 2). Differences in growth between regions began at about 3.5 years for common jack mackerel, with the resulting difference in L_∞ by age 13 being 4 cm FL (Fig. 4A). In redbait, growth differences began at approximately the same age as common jack mackerel (3 years versus 3.5 years, respectively; Fig. 4B), but the resulting difference in L_∞ was smaller for redbait (1 cm FL; KI: L_∞=249.52 cm FL [standard error (SE) 1.6]; NSW: L_∞=238.89 cm FL [SE 1.2]) than for common jack mackerel (4 cm FL; KI: L_∞=299.40 cm FL [SE 2.5]; NSW: L_∞=259.79 cm FL [SE 1.3]). Otolith growth at age from the mixed-effects model indicates that common jack mackerel and redbait from KI had faster growth than individuals from NSW (Fig. 4, C and D).

Intrinsic predictors of growth

Overall, growth synchrony for all growth comparisons was low and varied between *Year* and *YearClass*. Common jack mackerel from both KI and NSW had greater growth synchrony within *Year* (0.94% and 3.50%, respectively) than within *YearClass* (0.08% and 0.12%, respectively). In contrast, redbait growth synchrony was greater within *YearClass* (1.40% and 1.00% for KI and NSW, respectively) than within *Year* (0.17% and 0.60%, respectively).

The best random-effect structure was different for all models; they included *FishID* as a random effect and a

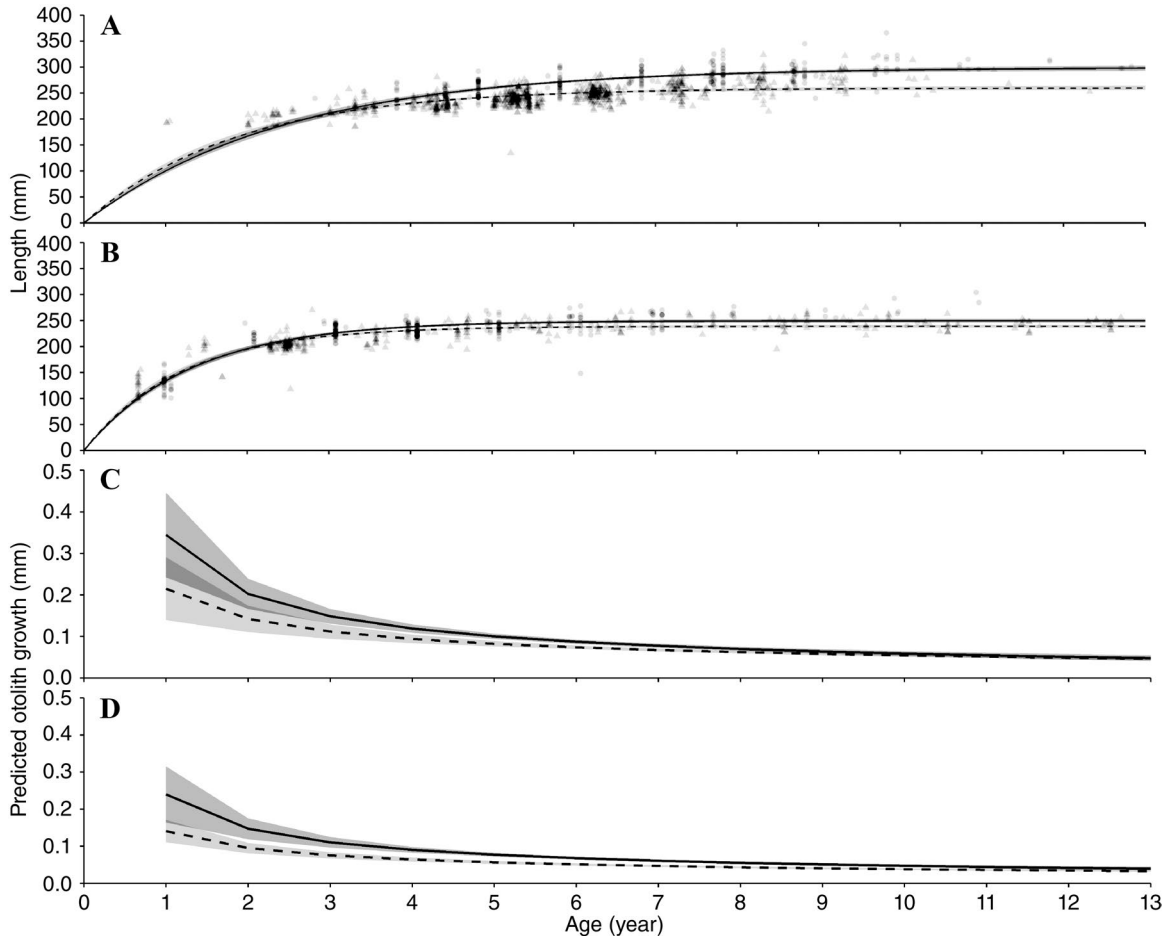

Figure 4

Von Bertalanffy growth curves for (**A**) common jack mackerel (*Trachurus declivis*) and (**B**) redbait (*Emmelichthys nitidus*) collected during 2014–2016 from waters off Kangaroo Island (KI; dark circles, solid line) and New South Wales (NSW; light triangles, dashed line) in Australia. Points indicate decimal ages based on presumed birth dates and collection dates. Also shown is predicted otolith increment growth (in millimeters) for (**C**) common jack mackerel and (**D**) redbait from KI (solid line) and NSW (dashed line). Shaded areas above and below the lines represent 95% confidence intervals.

Table 2

Estimates of von Bertalanffy growth parameters for common jack mackerel (*Trachurus declivis*) and redbait (*Emmelichthys nitidus*) collected off Kangaroo Island and New South Wales in Australia during 2014–2016. The parameters include the asymptotic length (L_∞) and the growth coefficient (k). Standard errors of the mean (SEs) are given in parentheses.

Species	Location	L_∞ (SE)	k (SE)
T. declivis	Kangaroo Island	299.40 (2.5)	0.41 (0.2)
T. declivis	New South Wales	249.52 (1.6)	0.77 (0.2)
E. nitidus	Kangaroo Island	259.79 (1.3)	0.54 (0.1)
E. nitidus	New South Wales	238.89 (1.2)	0.84 (0.2)

combination of the variables of *Year* and *YearClass*, with and without random slopes of *Age* and random intercepts (Suppl. Table 1). The best growth models that excluded environmental variables included only *Age* as a fixed effect (Suppl. Table 2). This was shown by the decrease in otolith increment growth (in millimeters per·year) as *Age* increased (Fig. 4, C and D).

Interannual variability in growth from the long-term mean ranged from −0.07 to 0.06 mm FL for common jack mackerel and from −0.02 to 0.04 mm FL for redbait. A pronounced increase in growth from the long-term mean occurred in 2013 for common jack mackerel from KI, and for both species from NSW, but not for redbait from KI (Fig. 5, A–D). Although a similar increase in growth was not observed for redbait from KI, a similar trend was observed the following year (Fig. 5C). Growth of redbait from NSW

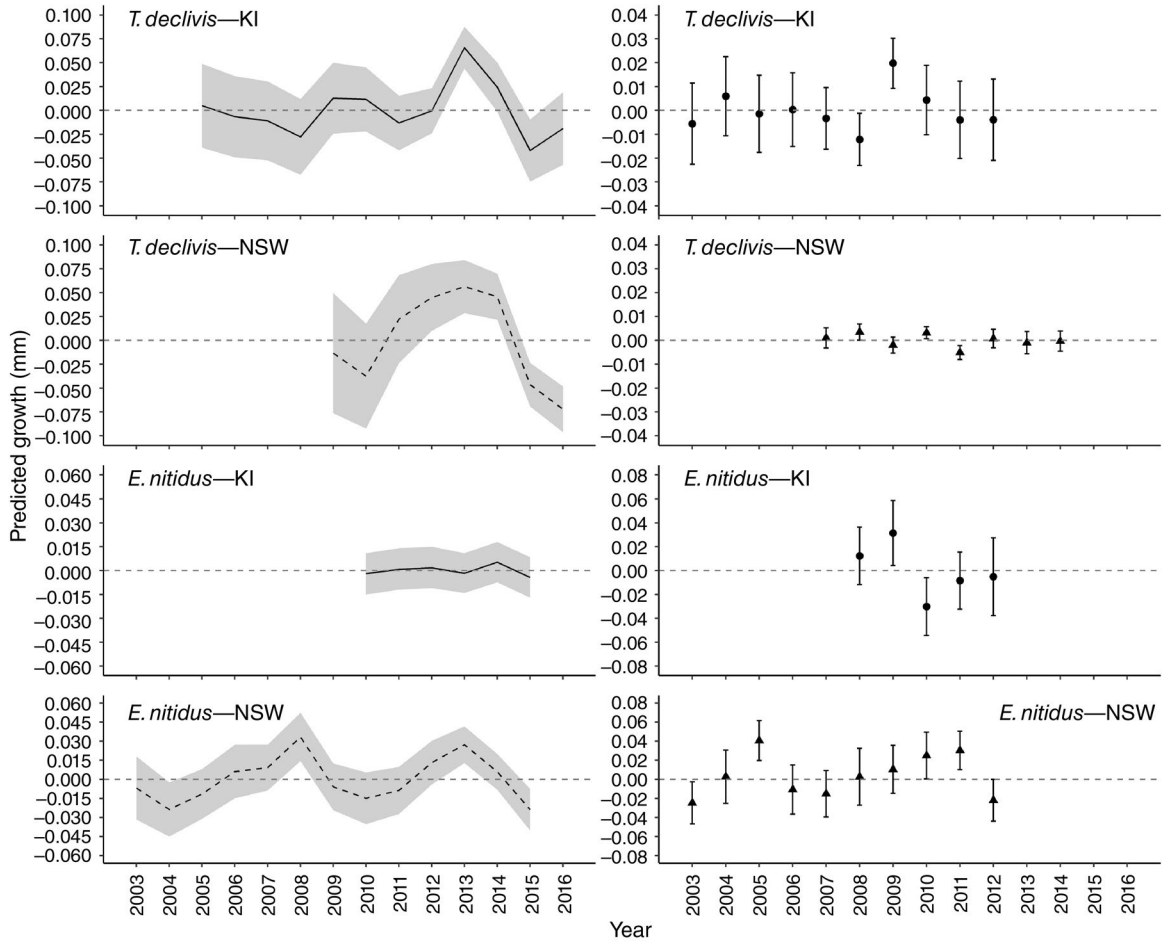

Figure 5

Panels on the left show predicted temporal variation (*Year*) in otolith increment growth relative to the long-term mean (indicated by the gray dashed line at the 0 value of the y-axis in each panel) for common jack mackerel (*Trachurus declivis*) and redbait (*Emmelichthys nitidus*) collected off Kangaroo Island (KI; black lines) and New South Wales (NSW; black dashed lines) in Australia. The shaded areas above and below the lines indicate standard errors of the mean. Panels in the right column show predicted temporal variation in otolith increment growth for common jack mackerel and redbait collected off KI (circles) and NSW (triangles) based on the birth date (*YearClass*) of fish relative to the long-term mean. Predicted variation in increment growth was produced from estimates of the *Year* and *YearClass* random effects (the best linear unbiased predictors). Error bars indicate standard errors of the mean. Note that values on the y-axis are different between species and for *Year* and *YearClass*. Common jack mackerel and redbait samples were collected between 2014 and 2016.

had higher interannual variation than that of redbait from KI, with the observed maximum predicted growth being approximately 4-fold that of fish from KI (Fig. 5, C and D). Redbait from NSW also had a pronounced increase in growth from the long-term mean in 2008, but common jack mackerel from KI had decreased growth compared with the long-term mean in the same year (Fig. 5, A and D).

YearClass variations in common jack mackerel from KI indicate that the 2009 cohort had greater growth than the long-term mean; all other cohorts had low variation between them (Fig. 5E). Conversely, the 2011 cohort of common jack mackerel from NSW had slower growth than the long-term mean (Fig. 5F). Three consecutive cohorts (2010–2012) of redbait from KI had slower growth than the long-term mean (Fig. 5G). Two *YearClass* cohorts of redbait from NSW had faster growth than the long-term mean (2005 and 2011; Fig. 5H).

Effects of environmental conditions

Chlorophyll-*a* concentrations and SSTs were both higher in NSW than off KI (0.56 mg/m^3 [SE 0.016] versus 0.22 mg/m^3 [SE 0.006] and 19.11°C [SE 0.14] versus 16.71°C [SE 0.11]). The top-ranked model assessing the effect of local environmental variables on growth for redbait from NSW and KI and for common jack mackerel from NSW was the base

model, which included no environmental variables (Table 3; Suppl. Table 3). When the difference in AIC_c between the current and top models (ΔAIC_c) indicated a high degree of support for numerous models (ΔAIC_c <2), AIC_c weight was examined to determine which model had the highest likelihood (Table 3). Common jack mackerel from KI were the only fish for which growth was associated with environmental conditions. The model that included SST had the highest AIC_c weight (0.96; Table 3, Suppl. Table 3), with predicted growth increasing 11.47% for every 1°C increase in SST in the range of 16.2–17.7°C (Fig. 6, A and B).

Discussion

In this study, the von Bertalanffy growth function and mixed-effects modeling were used to explore differences in the growth of small pelagic fishes between 2 temperate regions in southern Australia. Growth chronologies were produced from otolith increments of common jack mackerel and redbait caught off KI in South Australia and off southern NSW to explore regional differences in growth rates and to investigate the influence of local environmental conditions on the growth rates of both species in each region. This study is one of the few to apply growth chronology analyses to small pelagic fishes, and results indicate that common jack mackerel and redbait had lower growth synchrony than site-attached benthic or benthopelagic species. Consistent regional differences were also identified for both species, with fish from KI growing to greater lengths than fish from southern NSW. Age was the key intrinsic driver of growth detected across models, and each of the environmental factors selected for this study had limited influence on growth. Sea-surface temperature correlated with growth of common jack mackerel from KI, with no other correlations evident for the other species and regions.

Temporal growth synchrony (estimated with the interclass correlation coefficient) in both species and regions (0.17–3.50%) was low compared with that from other studies. For example, growth synchrony in species from similar regions has been reported as 2.0–21.6% in tiger flathead (*Platycephalus richardsoni*) (Morrongiello and Thresher, 2015), 0.4–13.7% in snapper (Martino et al., 2019), 0.1–15.0% in ocean perches (*Helicolenus* spp.) (Grammer et al., 2017), and 3.0–13.8% in black bream (Doubleday et al., 2015). The movement patterns of common jack mackerel and redbait may explain the low growth synchrony observed in our study. Results of studies on the reproductive biology of both species indicate frequent movements (Marshall et al., 1993; Welsford and Lyle, 2003; Ewing and Lyle, 2009), which expose them to a broad range of physical and biological conditions. In contrast, species that have previously been determined to have growth synchrony are mostly benthic species that tend to move over relatively small distances.

Table 3

Results from the full-fixed and intrinsic model fitted with local data for environmental variables, sea-surface temperature (SST) and chlorophyll-*a* (Chl-*a*) concentration, and used to examine growth of common jack mackerel (*Trachurus declivis*) and redbait (*Emmelichthys nitidus*) collected off Kangaroo Island (KI) and New South Wales (NSW) in Australia between 2014 and 2016. Models included the base model (full-fixed and intrinsic model), with values provided in the rows labeled *Growth*, and the base model fitted with SST or Chl-*a* concentration. Degrees of freedom (df), Akaike information criterion corrected for small sample size (AIC_c), the difference in AIC_c between the current and top models (ΔAIC_c), the proportion of the total predictive power of the model set (AIC_c weight [AIC_cWt]), log likelihood (LL), conditional coefficient of multiple determination (R^2_c), and marginal R^2 (R^2_m) are presented for each model. Values of R^2_c and R^2_m were calculated with the restricted maximum likelihood estimates of error. The top-ranked model for each species in each region is indicated with an asterisk (*).

Trachurus declivis

KI								NSW							
Model	df	AIC_c	ΔAIC_c	AIC_cWt	LL	R^2_m	R^2_c	Model	df	AIC_c	ΔAIC_c	AIC_cWt	LL	R^2_m	R^2_c
Growth	9.00	124.65	9.12	0.01	−53.19	0.50	0.72	Growth*	8.00	43.34	0.00	0.48	−13.48	0.61	0.73
+SST*	10.00	115.53	0.00	0.96	−47.59	0.54	0.73	+SST	9.00	44.00	0.66	0.35	−12.76	0.62	0.74
+Chl-*a*	10.00	122.31	6.78	0.03	−50.99	0.52	0.72	+Chl-*a*	9.00	45.43	2.09	0.17	−13.47	0.61	0.73

Emmelichthys nitidus

KI								NSW							
Model	df	AIC_c	ΔAIC_c	AIC_cWt	LL	R^2_m	R^2_c	Model	df	AIC_c	ΔAIC_c	AIC_cWt	LL	R^2_m	R^2_c
Growth*	8.00	45.84	0.00	0.52	−14.49	0.48	0.63	Growth*	9.00	250.18	0.00	0.42	−115.87	0.48	0.58
+SST	9.00	47.80	1.96	0.19	−14.36	0.48	0.63	+SST	10.00	250.44	0.26	0.37	−114.95	0.48	0.58
+Chl-*a*	9.00	47.01	1.17	0.29	−13.97	0.48	0.64	+Chl-*a*	10.00	251.53	1.35	0.21	−115.49	0.48	0.59

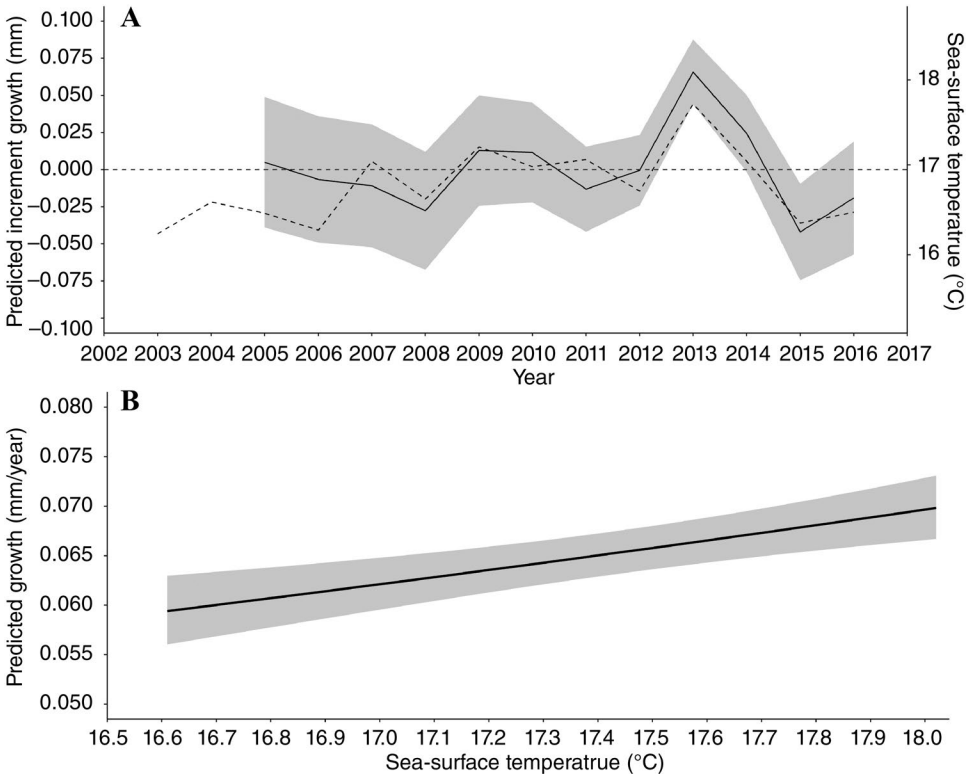

Figure 6

(**A**) Predicted temporal variation in otolith increment growth (solid line), relative to the long-term mean (gray dashed line) and to optimal local sea-surface temperature (black dashed line), and (**B**) sea-surface temperature predicted effects plot of otolith increment growth for common jack mackerel (*Trachurus declivis*) collected from waters off Kangaroo Island in Australia during 2014–2016. Predicted interannual growth variation is based on estimates for the *Year* random effect (best linear unbiased predictors). In panel A, the shaded area indicates standard error of the mean. In panel B, the shaded area indicates the 95% confidence interval.

Benthic species are more likely to be exposed to similar conditions and, therefore, have high growth synchrony among individuals, as seen in the growth synchrony of site-attached marine fishes, such as the tiger flathead (2.0–21.6%; Morrongiello and Thresher, 2015), and of sessile marine organisms, such as the Pacific geoduck (*Panopea abrupta*) (62–72%; Helser et al., 2012). In these cases, the minimal movement or lack thereof results in more consistent environmental conditions experienced across individuals, compared with the more variable and widespread movements of small pelagic fishes (Eiler and Bishop, 2016). In contrast, results of other studies in which the growth chronologies of small pelagic fishes were examined indicate synchrony in growth among individuals, and environmental effects on growth have been identified (Tanner et al., 2019). However, the species examined in other studies reside in shallow coastal waters (with depths of ~100 m); in contrast, the species investigated in our study occur at depths >100 m (Pullen and TDPIF, 1994; Welsford and Lyle, 2003; Tanner et al., 2019). As such, the low interclass correlation coefficients observed in our study may be a result of the deeper pelagic habitat of common jack mackerel and redbait causing less-defined increments compared with the habitat and increments obseved for other species (e.g., snapper or black bream) (Newman et al., 2000).

The challenges in reading growth increments on otoliths of common jack mackerel and redbait might have resulted in less precise measurements and, therefore, in artificially reduced synchrony. In the absence of cross-dating, the likelihood of errors in growth increment dating increases, possibly dampening extrinsic signals in increment data (Black et al., 2016; Smoliński et al., 2020). As a result, potential dating errors might have also contributed to the low synchrony observed (Smoliński et al., 2020).

Both species had higher growth synchrony off NSW than off KI. This finding may reflect the different oceanic processes of each region. The EAC originates in the Coral Sea and flows southward along the coast of NSW (Suthers et al., 2011). As the EAC separates from the coast, it forms a series of eddies (200–300 km in diameter) along the coastline that can persist for up to a year, and these eddies constitute a vital process for the nutrient cycling and biological

productivity in this region (Ridgway and Hill[4]). The large range and timescale in which eddies exist may facilitate the high growth synchrony observed in fish from NSW. In comparison, KI is influenced by the Flinders Current, a northern boundary current, and the Leeuwin Current, a seasonal shelf-break current (Middleton and Cirano, 2002; Middleton and Bye, 2007). This region is characterized by short events (3–10 d) of summer upwelling and winter downwelling along the southern coast of Eyre Peninsula, Bonney Coast, and western KI, resulting in increased productivity in these regions (Kämpf et al., 2004; Ward et al., 2006; Middleton and Bye, 2007). In comparison with the magnitude and temporal extent of the eddies in NSW, the smaller size and shorter period of the upwelling off KI may not have the strength to drive the growth synchrony in these fishes, likely explaining the difference in growth synchrony between these regions.

Both species grew larger off KI than off southern NSW. Such regional differences have previously been documented in several temperate fish species, including the Pacific sardine (Izzo et al., 2017), Australian salmon (*Arripis trutta*) (Hughes et al., 2017), and sand whiting (Stocks et al., 2011). Variation in available resources (e.g., food and habitat) can be the driving force that alters the demographics of a population (Ruttenberg et al., 2005; Hughes et al., 2017) and results in differences across their distributions. Although the diets of both common jack mackerel and redbait are similar across their distributions, with krill being their main prey item (Ward and Grammer[1]), differences in growth across their distributions were observed in our study—between populations of common jack mackerel and within the population of redbait (Ward et al.[9,10]).

The more variable growth in both species off NSW, in comparison to that off KI, can likely be explained by the EAC and associated eddies. Upwelling and biological productivity are driven by increases in vertical mixing of the epipelagic zone due to water circulation of eddies and their interaction with the continental shelf and coastline. As a result, environmental conditions vary among years depending on the extent of the EAC southward extension and ensuing location of eddies (Tilburg et al., 2001; Ridgway and Hill[4]). Findings of studies on the larval growth of Pacific sardine (Uehara et al., 2005), white trevally (*Pseudocaranx dentex*), and jack mackerel (*Trachurus novaezelandiae*) indicate the effects of the EAC and its upwelling regions on growth and the amount of interannual variability (interannual variability in increment growth relative to the long-term mean) among species (Syahailatua et al., 2011). In comparison, the reduced temporal and spatial scale of upwelling events off KI (Middleton and Bye, 2007), in combination with the lack of basin-wide changes, has likely resulted in the lower interannual variability in growth of fishes off KI than off NSW.

Similar to differences between regions, the higher interannual variability in growth of common jack mackerel compared with that of redbait in both regions may reflect the conditions they are exposed to in their respective habitats. Although the species occur in similar habitats, redbait are also found around seamounts, mid-ocean ridges, and islands and at deeper depths than common jack mackerel (Pullen and TDPIF, 1994; Welsford and Lyle, 2003). This difference in habitat means that common jack mackerel are more likely to be influenced by the environmental conditions of surface waters, which are in turn more likely to vary between years than the deeper waters in which redbait reside (Ridgway and Dunn, 2003). Because of this increased distribution depth, SST may not be the most appropriate temperature variable for redbait; however, bottom temperature records covering the chronologies in our study areas are not available. As such, SST is currently the most suitable proxy we have for temperature changes in these regions for the chronologies in this study.

The principle factor influencing somatic growth in ectotherms is commonly thought to be environmental temperature (Hughes et al., 2017). Marine organisms require specific temperature ranges to maintain control of physiological processes and avoid thermal stress (Calosi et al., 2008). In South Australia, snapper growth declined at temperatures higher than 18–20°C, which is the likely pejus temperature for snapper in South Australia (Martino et al., 2019). Results from the linear models in our study indicate that the optimal temperature for growth of common jack mackerel at KI is approximately 16–18°C (KI actual SST range: 16.42–18.01°C), a range at which the growth rate was still increasing. However, the growth rate of common jack mackerel at 18–20°C (NSW actual SST range: 18.40–20.05°C) was lower. This result indicates that a mean temperature higher than 18°C might start to cause some thermal stress, decreasing growth rates. Within the NSW region, the growth and metabolic costs of the red moki (*Chirodactylus spectabilis*) has already been affected by the intensification of the EAC (Neuheimer et al., 2011). As such, a continued increase in water temperature may result in the decline of the growth rates of common jack mackerel off NSW; however, a specific study investigating the thermal tolerance of common jack mackerel is required to define the optimal temperature for this species.

Indirect effects, such as changes in productivity (e.g., food), structure (e.g., habitat and abundance of predators), and composition (e.g., abundance of competitors), can also affect fish growth (Brander, 2010). For example, productivity or food availability can trigger massive changes in a population (Sánchez-Garrido et al., 2019), as has been reported for populations of anchovy and sardine species

[9] Ward, T. M., G. L. Grammer, A. R. Ivey, J. J. Smart, and P. Keane. 2018. Spawning biomass of jack mackerel (*Trachurus declivis*) and sardine (*Sardinops sagax*) between western Kangaroo Island, South Australia and south-western Tasmania. Report to the Australian Fisheries Management Authority. South Aust. Res. Dev. Inst., SARDI Publ. F2018/000174-1, SARDI Res. Rep. Ser. 983, 51 p. SARDI Aquat. Sci., Adelaide, Australia. [Available from website.]

[10] Ward, T., G. Grammer, A. Ivey, and J. Keane. 2019. Spawning biomass of redbait (*Emmelichthys nitidus*) between western Kangaroo Island, South Australia and south-western Tasmania in October 2017. Report to the Australian Fisheries Management Authority. South Aust. Res. Dev. Inst. SARDI Publ. F2019/000053-1, SARDI Res. Rep. Ser. 1011, 38 p. SARDI Aquat. Sci., Adelaide, Australia. [Available from website.]

in response to regime shifts in the Californian (Rodríguez-Sánchez et al., 2002), Humboldt (Alheit and Niquen, 2004), Benguela (Cury and Shannon, 2004), and Canary (Sánchez-Garrido et al., 2019) current systems. However, changes in Chl-*a* concentration did not affect growth of common jack mackerel and redbait in our study, and the observed differences may be the result of other indirect effects that we did not measure. The reason for the lack of effect of SST on growth of redbait is also unclear.

Because redbait reside in deeper waters than common jack mackerel, the influence of environmental variables, such as SST, on their growth may be reduced (Welsford and Lyle, 2003; Thresher et al., 2007). This reduction in influence of environmental conditions indicates a limitation of our study: the model is limited to a small number of available local variables. In addition, the AIC_c weight does not provide overwhelming support for one candidate model for each species and region, indicating that some models are equally supported. Other factors, not included in this study, are likely driving the growth of common jack mackerel and redbait and can be an avenue for future research. Possible model extensions could include an upwelling index as a measure of the strength and productivity in upwelling events within these regions. Furthermore, inclusion of an index of EAC strength and extent would enable testing whether, and to what magnitude, the EAC may be affecting these species in NSW.

Conclusions

Here, we reveal inter-regional differences in the growth of common jack mackerel and redbait, differences we hypothesize to be linked to the EAC and associated eddies off NSW and to upwelling events off KI. The environmental variables examined (SST and Chl-*a* concentration) had little effect on growth with the exception of common jack mackerel from KI. These populations and the fisheries they support, therefore, may be more resilient to some environmental changes than has previously been assumed. However, further investigation is required to better understand the environmental drivers of growth in these populations and to assess the potential effects of climate variations over long time periods. Increasing the sample size is needed to lengthen the time series and to increase sample depth. Additional environmental factors, such as an upwelling index or intensity and extent of the EAC, should be included in future models to improve the amount of deviance explained and provide a better understanding of the factors driving growth in these small pelagic fishes. Growth chronologies, such as those that we present here, are useful for identifying the effects of environmental conditions on fish growth and can be incorporated into stock assessments to inform the management of fisheries.

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